SIX STRIDULATING ORGANS ON ONE SPIDER (ARANEAE, ZODARIIDAE): IS THIS THE LIMIT?

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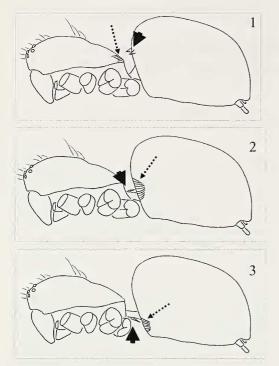
ABSTRACT. A new type of stridulatory organ is described and figured occurring in three species of *Mallinella* Strand from Thailand and Singapore. In one species there are four stridulatory organs, with the ridges on femora I and II and the pegs in the shape of granulations on femora II and III. In both the other species an additional pair occurs, with ridges on femora III and pegs on femora IV. To date no more than four stridulatory organs have been recorded on a single spider. Examples of various known forms of stridulatory organs on spiders are illustrated and their significance briefly discussed.

Keywords: Stridulation, Thailand, Singapore, courtship, mate check

Stridulating organs are manifold in spiders and were reported for at least 22 families of spiders in Uetz & Stratton (1982) and since then, several cases in other families (Corinnidae, Tetragnathidae, Zodariidae, see below) have been mentioned. Some of the organs are single, but paired stridulatory organs appear to occur more commonly. These organs inevitably comprise two elements: the "pars stridens", a sclerotized area provided with a series of ridges referred to as "the file" or simply "the ridge" in those cases where there is only one, and the "plectron" which may be one or a series of stiff setae or pegs, sometimes called "the plectrum" or "the scraper" in the case of a single peg.

In single stridulatory organs, sounds are produced by rubbing the front of the abdomen against the rear of the cephalothorax, the surfaces of which are provided either with ridges, pegs or stiff setae (Figs. 1-3) (e.g. Maddison & Stratton 1988a, b). The same applies to the sound produced by files on the inner surface of the chelicerae that occurs in Mygalomorphae or on the inner surface of the anterior lateral spinnerets as found in some Theridiidae (Forster et al. 1990; Agnarsson 2004). Paired stridulatory organs, usually in the form of ridges and pegs, occur in many other taxa. Most commonly, these ridges occur on the chelicerae (externally), and are rubbed by the palps; on the booklung covers, rubbed by the fourth legs; or on the coxae of the first legs rubbed by a peg on the second trochanters (e.g. Hinton & Wilson 1970). Rovner (1975) recorded a stridulatory device in males of Lycosa and Schizocosa: a plectrum on the male palpal tibia rubs against a file on the cymbium. Edwards (1982) later found a similar device in the salticid Phidippus mystaceus (Hentz). Legendre (1963) and Uetz & Stratton (1982) provided a fairly complete overview of the different types of stridulatory organs, summarized here in Figs. 1–10. Starck (1985) gave a complete list of the known stridulatory organs, analyzed the structure of the elements that compose a stridulating organ and discussed the function and the evolutionary aspects of the devices. He stressed the homoplasy of these structures in different taxa and concluded that there has been parallel development of similar organs, even within the same family.

Since these early papers, several more types of stridulatory organs have been described. Maddison (1987) found Marchena minuta (Peckham & Peckham 1888) and other jumping spiders (Salticidae) to be provided with ridges or a row of stout setae on the dorsal base of the femora I combined with respectively a row of setae or a stridulatory file on the carapace just under the eyes. Simon (1937) was apparently aware of this structure and mentions the femoral tubercles in Icius Simon. Wunderlich (1995) reported on an external longitudinal ridge on the chelicerae in Zygiometella Wunderlich (Tetragnathidae), supposedly combined with setae on the inner side of the male palp to form a stridulatory organ. Ramirez et al. (2001) found a similar



Figures 1–3.—Examples of spiders with one stridulatory organ (appendages omitted). 1. *Steatoda* Sundevall (Theridiidae), with file on carapace, pegs on abdomen; 2. *Cambridgea* L. Koch (Stiphidiidae), with file on abdomen, pegs on pedicel (dorsally); 3. *Cambridgea* L. Koch (Stiphidiidae), with file on abdomen, pegs on pedicel (ventrally) (after Legendre 1963 and Uetz & Stratton 1982). Dotted arrows = files and ridges, solid arrows = pegs.

stridulating system in *Olbus* Simon 1880 (Corinnidae): a retrolateral ridge on femur IV corresponding with a field of modified seta bases on the abdomen. This organ combines with a field of prolateral setae with modified bases on the prolateral side of the same femur opposed to a field of evenly spaced setae with transversely arranged bases. If both these combinations represent stridulating organs, this was the first case reported of four such organs in a spider.

Only one putative stridulating organ was so far reported in the Zodariidae: the species *Akyttara homunculus* (Jocqué 1991) has warts on the anterior surface of the abdomen corresponding with ridges on the posterior part of the carapace (Jocqué1991).

The present paper reports on a remarkable case of multiple stridulatory organs and pro-

vides a concise overview of the present knowledge on these structures.

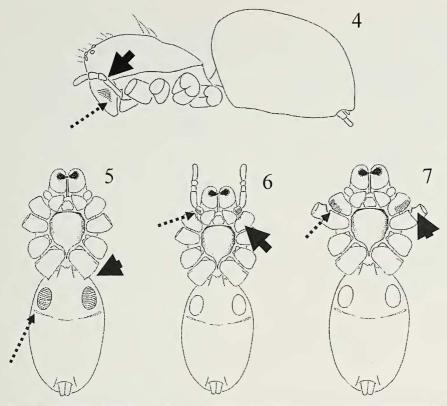
METHODS

Stridulating organs on the femora of Mallinella Strand 1906 (Zodariidae) were noted for the first time while sorting through collections of representatives of the family from Thailand collected by P. Schwendinger. A dark area around the stridulating file of the species with four stridulating organs made that region conspicuous. Without the color contrast, the structures would probably have passed unnoticed. Stridulatory structures were found on the males of two species; each species was represented by only one male. A more interesting example was found in the collection of J. Murphy. This collection included both sexes of what appeared to be M. cinctipes (Simon 1892) according to the drawing of the epigyne in Workman (1896) and a photo of the spider by Koh (1989).

All the examined specimens belong to the palaeotropical genus *Mallinella* that has a vast distribution from West Africa to northern Australia (Jocqué 1993). They are typical forest soil-dwellers and compulsory termite feeders that hide in silk-lined spherical buried retreats during daytime.

Specimens examined.—Mallinella sp. 1: 1∂ (with four stridulatory organs), Thailand, Penang Hill, 150-330 m, 02.xii.1991 (P. Schwendinger). Mallinella sp. 2: 1♂ (with six stridulatory organs), Thailand, Doi Chiang Dao, 510 m, 25.x-23.xi.1990 (P. Schwendinger). Mallinella cinctipes: 1 8: Singapore, Upper Pierce Reservoir, iii.1986 (Murphy collection 13418); 16: Singapore, Upper Pierce Reservoir, ii.1988 (Murphy collection 15443); 3∂, 1♀: Singapore, Bukit Timah, ii.1988 (Murphy collection 15471). The voucher specimens of the unknown species from Thailand shall be deposited in the Musée d'Histoire Naturelle de Genève, Switzerland. Males were preserved in ethanol 75% in the field and examined in the lab.

The male specimen from Penang Hill was scanned using a XL30 ESEM scanning electron microscope in wet mode with cooling cell that leaves the specimen undamaged. Images (Fig. 13) were taken of the entire specimen at different depths and composed into a single photomontage by using an analogue camera and composition software. (Automontage of



Figures 4–7.—Examples of spiders with two stridulatory organs (appendages omitted). 4. Linyphiidae, Hahniidae (and many other families), with file on chelicerae, pegs on palps; 5-. Linyphiidae, with file on abdomen (ventrally), pegs on leg IV; 6. Linyphiidae, with file on palps, pegs on coxae I; 7. Linyphiidae, with file on coxae I, pegs on trochanters II (after Legendre 1963).

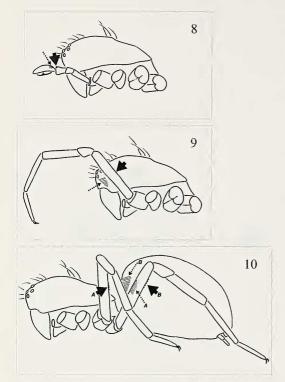
Synoptics). Other SEM images were taken with a JEOL 6480LV.

RESULTS

Mallinella sp. 1 (Figs. 11, 13) appears to have four and Mallinella sp. 2 and Mallinella cinctipes (Fig. 12) appear to have six stridulatory organs. In the latter, the ridges are situated on a conspicuous swelling (Figs. 15, 16) of the dorsal base of the anterior femora and are apparently rubbed by prolateral ventral granulations (Fig. 18) at the base of tiny setae on the following femur. In Mallinella sp. 1, the file area is rounded and has a diameter of 0.45 mm, with 48 ridges which means that the ridges are slightly less than 0.01 mm apart. The granulations are 0.045 mm apart. In Mallinella sp. 2 the ridges are somewhat thinner (52 in an area with diameter 0.41 mm) and the granulations more densely set at a distance of just under 0.01 mm. In Mallinella cinctipes the stridulation area on Fe II is on average 0.34 mm across and has 72 ridges which means that they are again thinner and about half as far apart as in the first species (5 μ m). The granulations are between 0.04 and 0.06 mm apart. The female of *M. cinctipes* has not the slightest indication of a femoral stridulation organ.

DISCUSSION

To date, no spider species with more than four stridulatory organs has been reported. The only probable case is that of *Olbus jaguar* Ramirez et al. 2001 mentioned in the introduction. As far as I am aware, no cases exist in which a single central stridulatory organ is combined with a symmetrical double organ. The number of stridulatory organs on a single spider is now known to be 1, 2, 4 or 6. The last two mentioned cases are especially surprising, as even in the case of other animals, such a high number has apparently never been recorded. The organ depicted here bears some



Figures 8–10.—8. Lycosidae, file on cymbium, peg on palpal tibia (after Rovner, 1975); 9. Salticidae, with file on side of carapace under the eyes, pegs on inner side of first femur (after Maddison, 1987). Dotted arrows = files and ridges, solid arrows = pegs; 10. Example of a spider with four stridulating organs and the only one known with a mixed set-up: *Olbus jaguar* (Corinnidae). One system (A) consists of a file on femur IV and pegs on femur III, the other one (B) of a file on the abdomen and pegs on femur IV (after Ramirez et al. 2001). Dotted arrows = files and ridges, solid arrows = pegs.

resemblance to those mentioned in *Olbus* and in *Marchena* Peckham & Peckham described by Maddison (1987) but in the zodariids the carapace and the abdomen are smooth and devoid of setae or ridges. In the *Mallinella*, the file is dorsolateral (Figs. 11, 12, 14–16) and directed towards the following femur with the granulations that apparently function as pegs. This is corroborated by the fact that the seta bases on the first femur (Fig. 17) have no granulate extensions whereas those of femora II, III and in some cases IV do (Fig. 18).

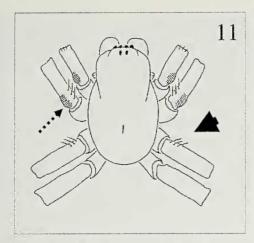
Stridulation may have two clearly different functions, i.e. defense and courtship (Starck 1985; Uhl & Schmitt 1996). Although there are no studies available for spiders with more

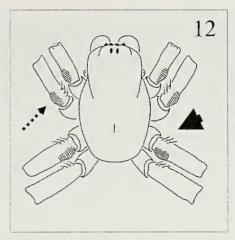
than two stridulatory organs, there is no reason to expect that the function should be different for multiple organs.

Defense stridulation in larger animals, such as mygalomorphs (Legendre 1963), is often audible to the human ear. However, in araneomorph spiders, stridulation probably originated as part of courtship (Starck 1985). Several hypotheses have been formulated regarding the function of this stridulation during courtship. These include mate recognition, antagonistic behaviour between males (Gwinner-Hanke 1970; Maddison & Stratton 1988a). stimulation of the female by the male (Eberhard 1996) and information transfer (Jocqué 1998). It is difficult to accept that more than one stridulating organ would be needed if the aim is to recognize the partner: the possibilities for variation with one "instrument" are endless and it is therefore unlikely that multiple stridulation organs are developed for that purpose. Stimulation of the partner is another possibility that has been invoked to explain the development of secondary sexual organs. The question always remains why species with similar morphology and life style would evolve such different degrees of partner stimulation.

"Mate check," (Jocqué 1998, 2002) on the other hand, assumes that the quantity of information transferred during courtship is directly related to the ecological specialization of the species. Via an array of signals, combined in a so-called "mating module" (Jocqué 2001, 2002), the presence of crucial adaptations in the male mate is verified during courtship and mating. In the speciose genus *Mallinella*, species of which have a highly specialized biology, the development of a complex stridulatory apparatus as part of the mating module is a plausible explanation certainly because the females appear to be devoid of such organs.

Another fascinating question to be answered is how these stridulatory organs are operated. It is very unlikely and physically apparently impossible that they are all activated at the same time in an orchestra-like manner. It is therefore to be expected that the organs are activated consecutively and in pairs, one on either side of the animal. This prompts the question whether spiders with more than six stridulating organs can be expected. If the organs are arranged as in *Olbus jaguar* (see



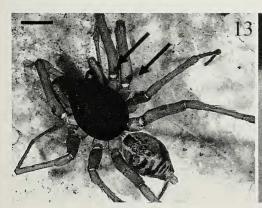


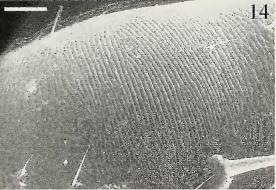
Figures 11–12.—Example of a spider with four and six stridulatory organs. 11. *Mallinella* sp. 1 (Zodariidae), with files on femora I and II, pegs on femora II and III; 12. *Mallinella* sp. 2 (Zodariidae), with files on femora I, II and III, pegs on femora II, III and IV. Dotted arrows = files and ridges, solid arrows = pegs.

above) a total of eight belongs to the possibilities. The arrangement in that species gives the impression that different types of stridulatory organs are present in one spider. Yet, as in the Mallinella, it can be expected that the movement involved is similar for both pairs: moving the femur with the pegs relative to the adjacent file. The main difference with the situation in Olbus is that in Mallinella the pegs are behind the file and it is difficult to imagine that a series of pegs would evolve on the abdomen. In Olbus it is the other way round and the last femur scratches a file on the abdomen. In this way it is possible to have four stridulating files on the same side operating them in sequence and with the same movement, like it must be the case for the organs in M. cinctipes. A spider with an eight instrument orchestra thus theoretically belongs to the possibilities.

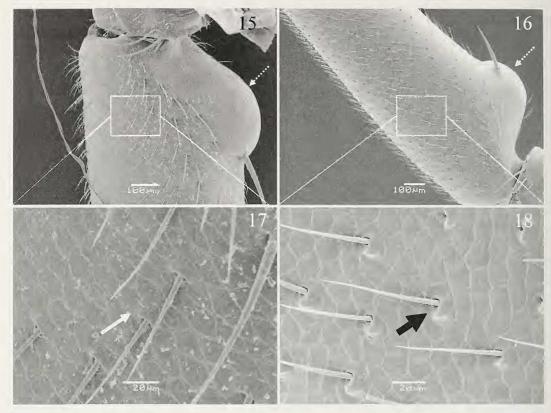
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Figures 13-14.—Mallinella species 1 from Thailand δ . 13, Habitus with arrows indicating files on femoral base I and II; 14. Stereoscan micrograph of femoral file. Scale bars = 1 mm (13); 0.1 mm (14).



Figures 15–18.—Mallinella cinctipes Singapore &. 15. Left femur I showing dorsal swelling with stridulating file (dotted arrow); 16. Right femur II showing dorsal swelling with stridulating file (dotted arrow); 17. detail of Fig. 15 showing knobless hair bases (white arrow); 18. detail of Fig. 16 showing pegs in the shape of a knob at hair base (solid black arrow).

LITERATURE CITED

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological journal of the Linnean Society 141:447–626.

Eberhard, W. G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Chichester, West Sussex, 501 pp.

Edwards, G.B. 1982. Sound production by courting males of *Phidippus mystaceus* (Araneae: Salticidae). Psyche 88:199–214.

Forster, R. R., N. I. Platnick & J. Coddington. 1990. A proposal and review of the spider family Synotaxidae (Araneae, Araneoidea), with notes on theridiid interrelationships. Bulletin of the American Museum of Natural History 193:1–116.

Gwinner-Hanke, H. 1970. Zum Verhalten zweier stridulierender Spinnen, *Steatoda bipunctata* Linné und *Teutana grossa* Koch (Theridiidae, Araneae), unter besonderer Berücksichtigung des Fortzpflanzungsverhaltens. Zeitschrift für Tierpsychologie 27:649–678.

Hinton, H.E. & R.S. Wilson. 1970. Stridulatory or-

gans in spiny orb-weaver spiders. Journal of Zoology of London 162:482–484.

Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201:1–160.

Jocqué, R. 1993. "We'll meet again", an expression remarkably applicable to the historical biogeography of Australian Zodariidae. Memoirs of the Queensland Museum 33:561–564.

Jocqué, R. 1998. Female choice, secondary effect of "mate check"? A hypothesis. Belgian Journal of Zoology 128:99–117.

Jocqué, R. & T. Szüts. 2001. Bacelarella (Araneae, Salticidae) in eastern Côte d'Ivoire: salticid radiation in a poorly lit environment. Annales du Musée royal de l' Afrique centrale 285:93–99.

Jocqué, R. 2002. Genitalic polymorphism—a challenge for taxonomy. Journal of Arachnology 30: 298–306.

Koh, J. 1989. A Guide to the Common Spiders of Singapore. Singapore Science Centre 160 p.

Legendre, R. 1963. L'audition et l'émission de sons chez les Aranéides. Annales de Biologie 2:371–390.

- Maddison, W. 1987. *Marchena* and other jumping spiders with an apparent leg-carapace stridulatory mechanism (Araneae: Salticidae: Heliophaninae and Thiodininae). Bulletin of the British Arachnological Society 7:101–106.
- Maddison, W.P. & G.E. Stratton. 1988. Sound production and associated morphology in male jumping spiders of the *Habronattus agilis* species group (Araneae, Salticidae). Journal of Arachnology 16:199–211.
- Maddison, W.P. & G.E. Stratton. 1988. A common method of sound production by courting jumping spider (Araneae, Salticidae). Journal of Arachnology 16:267–269.
- Ramirez, M.J., L. Lopardo & A.B. Bonaldo. 2001. A review of the Chilean spider genus *Olbus*, with notes on the relationships of the Corinnidae (Arachnida, Araneae). Insect systematics and evolution 31:441–462.
- Rovner, J.S. 1975. Sound production by nearctic wolf spiders. A substratum-coupled stridulatory mechanism. Science 190:1309–1310.
- Simon, E. 1937. Les arachnides de France. Tome VI. Synopsis générale et catalogue des espèces

- françaises de l'ordre desAraneae; 5e et derniére partie. Paris, 6:979–1298.
- Starck, J.M. 1985. Stridulationsapparate einiger Spinnen—Morphologie und evolutionsbiologische Aspekte. Zeitschrift für zoologische Sytematik und Evolutionsforschung 23:115–135.
- Uetz G.W. & G.E. Stratton. 1982. Acoustic communication and reproductive isolation in spiders. Pp. 123—159. *In P. Witt & J. Rovner*, eds. Spider Communication. Mechanisms and Ecological Significance. Princeton University Press.
- Uhl, G & M. Schmitt. 1996. Stridulation in *Palpimanus gibbulus* Dufour (Araneae, Palpimanidae). Revue Suisse de Zoolologie. hs. 649–660.
- Workman, T. 1896. *Malaysian spiders*. Vol. I. Belfast, pp. 25–104.
- Wunderlich, J. 1995. Beschreibung der neuen Spinnen-Gattung *Zygiometella* der Tetragnathidae: Metinae und eines bisher unbekannten Typs von Stridulations-Organen (Arachnida: Araneae). Beiträge zur Araneologie 4:639–642.
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